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Herbivore-mediated structural diversity of vegetation

Ruifrok, Jasper Laurens

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Chapter 2: Formation and maintenance of vegetation mosaics by free-ranging herbivores: importance of abiotic variation and herbivore size

Jasper L. Ruifrok, Max Rietkerk, Maarten B. Eppinga, Han Olff, Christian Smit

Abstract

Free-ranging herbivores are increasingly introduced in European nature areas to form and maintain heterogeneous vegetation mosaics that typically consist of patches of lawn (short, high quality and frequently grazed) alternating with patches of rough (tall, low quality and infrequently grazed). However, the desired vegetation mosaics are not always achieved and the underlying processes are poorly understood. We investigate how mosaic formation and maintenance depends on herbivore size and abiotic variation (e.g., the spatial distribution of water availability, soil aeration or salinity). We made a spatially explicit model incorporating herbivore size (small, medium, large), hierarchical foraging by herbivores, clonal invasion by rough plants and abiotic variation. The results suggest that without abiotic variation small herbivores are more likely to form vegetation mosaics than large herbivores, as large herbivores can tolerate low quality plant material and thus forage frequently on roughs. Furthermore, without abiotic variation, mosaics lose their heterogeneity (variation is patch shape and size), due to hierarchical foraging by herbivores and clonal invasion by rough plants. Abiotic variation (simulated by patches with different growth rates) positively affects maintenance of the mosaic, because small tall rough patches that have high growth rate can better cope with high grazing frequency, while small lawn patches with low growth rate can better cope with low grazing frequency. Interestingly, the presence of abiotic variation seems to increase the likelihood that also large herbivores can form and maintain heterogeneous lawn-rough mosaics. This insight is important for the numerous conservation and restoration programs with free-ranging herbivores in European nature areas. It suggests that herbivores will ultimately have a more positive effect on associated biodiversity in abiotically more heterogeneous landscape.

2.1 Introduction

Free-ranging herbivores are increasingly introduced for conservation reasons in former European agricultural areas to promote heterogeneous vegetation mosaics with a wide variety of patch sizes and shapes (Olff et al. 1999; Adler et al. 2001; Van Uytvanck et al. 2008). Such lawn-rough mosaics are a common feature in grazed ecosystems, and consist of short lawns that alternate with patches of tall rough vegetation (Adler et al. 2001). Lawn patches are generally dominated by short plant species with a rosette or stoloniferous architecture

(Díaz et al 2007; Stock et al. 2009) and have a high grazing tolerance (McNaughton 1984; Rosenthal and Kotanen 1994). Rough patches are generally dominated by tall plant species that have an erect or tussock architecture and therefore are stronger light competitors (Díaz et al., 2007; Stock et al. 2009). The structural diversity of these vegetation mosaics affects many ecosystem functions and services (Turner 1989; Turner et al. 1989) and generally has positive effects on plant and animal diversity (Palmer 1994; Olff et al. 1999). However, introduction of free-ranging large herbivores does not always lead to the desired formation of heterogeneous vegetation mosaics. In some cases the vegetation structure remains rather homogeneous or the mosaic consists of only a few large patches (Adler et al. 2001; Laca et al. 2010). Processes behind these variable results are thus far poorly understood. A better understanding of the underlying mechanisms is crucial for the numerous conservation and restoration programs with free-ranging herbivores in European nature areas.

De Knegt et al. (2008) showed that two processes are crucial for the formation of vegetation mosaics by herbivores, self-facilitation and hierarchical foraging. Self-facilitation is the process by which grazing increases and maintains nutritional quality of plant communities, and thus is essential for the formation and maintenance of lawn patches (McNaughton 1984). The increase of plant quality by grazing tends to occur in the short term because grazed plants produce new shoots that contain fewer structural compounds and have a high phosphorus and nitrogen content (Augustine and McNaughton 1998; Anderson et al. 2007). In the long term grazing increases the nutritive quality of the vegetation as it favors short plant species, which contain relatively little structural compounds such as fibers (Rosenthal and Kotanen 1994; Díaz et al. 2007; Kuijper et al. 2008). Hierarchical foraging is the process by which herbivores select patches on various spatial and temporal scales (Senft et al. 1987). The result of hierarchical foraging is that feeding stations are likely to be grazed when adjacent feeding stations are grazed (De Knegt et al. 2008). Research has shown that due to hierarchical foraging, herbivores can form patches even when there are no clear initial patches present (De Knegt et al. 2008). Hence, due to the combination of these two processes - self-facilitation and hierarchical foraging - free-ranging herbivores can generate vegetation mosaics, even from homogeneous starting conditions (De Knegt et al. 2008).

Although hierarchical foraging is crucial for generating vegetation mosaics, in the long run hierarchical foraging might have negative effects on the heterogeneity of the mosaic. Small rough patches surrounded by lawn might disappear when they are accidentally grazed together with the focal lawns, a process that is called associational palatability (Atsatt and Dowd 1976). Similarly, small lawn patches surrounded by rough vegetation may disappear as they are more often ignored due to their small size, a process called associational resistance (Atsatt and Dowd 1976; Olff et al. 1999), resulting in low grazing frequency and high competition for light with rough plants (Ritchie and Olff 1999; Laca et al. 2010), especially when rough species can clonally invade lawn patches (Kuijper et al. 2004). Consequently, hierarchical foraging, in combination with clonal invasion, may act as a homogenizing force in the long run, as it dissolves all small patches which merge into a few large patches.

Herbivore size is another important factor that may influence the formation of lawn-rough mosaics. Firstly, herbivore body size interacts with hierarchical foraging. Large herbivores have a larger grain size at which they sample their environment (Ritchie

and Olff 1999). Therefore, large herbivores tend to ignore small patches more often than small herbivores (Laca et al. 2010). Secondly, large herbivores (biomass range 400 – 500 kg, equivalent of cattle) can generally cope with lower quality forage compared to smaller sized herbivores (biomass 50 – 100 kg, equivalent of sheep) due to differences in their digestive tract (Hopcraft et al. 2010). Consequently, the differences in quality between lawn and rough are less pronounced for large herbivores than for smaller herbivores. As a result of these two reasons, smaller herbivores (e.g. sheep) may be better in creating and maintaining vegetation mosaics than large herbivores (e.g. cattle).

The role of the spatial variation in abiotic factors that affect plant growth (e.g. water availability, salinity and soil oxygen - from here on abiotic variation) for the formation of lawn-rough mosaics has been thus far little explored, while it may importantly counteract the homogenizing force of hierarchical foraging and clonal invasion. Abiotic variation may strongly affect lawn-rough mosaic formation because plant growth strongly affects how plants cope with grazing (Olff et al. 2002). For example, if plant growth is positively affected by abiotic factors (leading to a high extrinsic growth rate), plants can quickly overcome the negative effect of grazing due to fast production of structural compounds (e.g. lignin), which quickly reduces their quality (Augustine and McNaughton 1998). If plant growth is negatively affected by abiotic factors (leading to a low extrinsic growth rate), plants can only slowly overcome the effect of grazing as it will take relative long before new structural compounds can be produced, meaning that plant quality declines more slowly after grazing. Hence, a heterogeneous distribution of abiotic factors may positively affect the formation of stable heterogeneous lawn-rough mosaics: small rough patches with a high extrinsic growth rate might sustain a relatively high frequency of (accidental) grazing without being transformed into lawn, whereas small lawn patches with low extrinsic growth rate might sustain a relatively low frequency of grazing without being transformed into rough vegetation. As accidental grazing of small rough patches and neglectance of small lawn patches is expected to occur more frequently with large (unselective) herbivores, abiotic variation might be more important for mosaic formation with large herbivores than with small herbivores.

In this study we made a spatial explicit model to investigate the importance of abiotic variation for mosaics formation and maintenance by different-sized herbivores. We hypothesized that (1) abiotic variation is important for formation and maintenance of vegetation mosaics and (2) more so with large herbivores than with small herbivores. Finally we discuss the generality of our findings in the light of conservation and restoration projects of grazed European grasslands

2.2 Methods

2.2.1 The model

Our model describes a plant community (P [g m⁻²]) on a 2D model domain Ω , which is discretized into a grid of m by n cells, each cell representing 1 m². In a cell, plant density changes due to growth, grazing and clonal dispersal. Growth in a focal cell, ($p(P[x,y])$ [g m⁻² d⁻¹]), is influenced by the amount of light that is absorbed and thus influenced by the plant density present in a cell. Grazing in a focal cell, ($g(P[x,y],P_D)$ [g m⁻² d⁻¹]) is also influenced by the plant density present in the focal cell, but also by the relative preference

of that cell, which is influenced by plant density over the whole grid (P_Ω). Clonal invasion is described by diffusion (Rietkerk et al. 2002); if cells with high plant density (rough) neighbor cells with low plant density (lawn) they invest a large part of their resources on clonal invasion to their neighboring cell. The full model reads:

$$\frac{dP_{[x,y]}}{dt} = p(P_{[x,y]}) - g(P_{[x,y]}, P_\Omega) + D\Delta P, \quad 2.1$$

where D [$\text{m}^2 \text{d}^{-1}$] is the clonal invasion rate.

Growth, the first term in equation 1, $p(P_{[x,y]})$, is based on the integration of photosynthesis over plant height using the Lambert-Beer equation (Huisman and Weissing 1994; Huisman and Olff 1998):

$$p(P_{[x,y]}) = \frac{\theta}{\kappa} \cdot \ln \left(\frac{l_{half} + l_{in}}{l_{half} + l_{out}(P_{[x,y]})} \right) - \delta \cdot P_{[x,y]}, \quad 2.2$$

where θ [d^{-1}] is extrinsic growth rate and thus determined by abiotic factors, κ [$\text{m}^2 \text{g}^{-1}$] the light extinction coefficient, and l_{half} [$\mu\text{mol photons m}^{-2} \text{s}^{-1}$] the half saturation constant for light. l_{in} [$\mu\text{mol photons m}^{-2} \text{s}^{-1}$] is the incoming light intensity and δ is the rate at which plant mass decreases due to metabolism and mortality. $l_{out}(P_{[x,y]})$ is the light intensity that is left after it has penetrated through the column of plant tissue, which is given by the Lambert-Beer equation:

$$l_{out}(P_{[x,y]}) = l_{in} \cdot \exp(-\kappa \cdot P_{[x,y]}), \quad 2.3$$

Grazing, the second term in equation 2.1, follows a functional response type II (asymptotic) (Bergman et al. 2001) with plant height ($s(P_{[x,y]})$ [m]), As the rate of herbivory is directly determined by plant height and not plant density (Van der Graaf et al. 2005). Grazing is therefore modeled as:

$$g(P_{[x,y]}, P_\Omega) = \iota \cdot \left(\frac{s(P_{[x,y]})}{s(P_{[x,y]}) + s_{half}} \right) \cdot h(P_{[x,y]}, P_\Omega), \quad 2.4$$

where ι [d^{-1}] is maximum daily intake per gram herbivore. s_{half} [m] is the half saturation constant for intake and $h(P_{[x,y]}, P_\Omega)$ is herbivore density. Herbivore density is the herbivore density averaged over a long time period. If the local herbivore density is 50 g m^{-2} , it means that a 500 kg herbivore spends 1/10,000th of its foraging time in this cell and thus is a measure for the frequency of grazing. Plant height is given by:

$$s(P_{[x,y]}) = s_m \cdot \left(\frac{P_{[x,y]}}{P_m} \right)^2, \quad 2.5$$

where s_m [m] is the plant height when the plant density equals P_m [g m^{-2}]. We implemented this nonlinear relation between plant density and plant height to model the high grazing

tolerance of short lawn patches. When intake is now plotted against plant density, grazing follows a functional response type III (sigmoid) (Holling, 1959a, b). Due to this functional response type III, intensity grazed lawn patches remain their high quality and stability, even at high grazing frequency (see supplementary materials).

Herbivore density is determined by the relative preference for the cell. Preference is the product of ingestion and digestion. Ingestion (grazing rate) is positively influenced by plant height (eq. 2.4). On the other hand, digestion is influenced by quality, and thus negatively related to plant height. Consequently, preference has an optimum (the forage maturation hypothesis) (Fryxell 1991). We calculate the preference $q(P_{[x,y]})$ [-] by:

$$q(P_{[x,y]}) = \frac{s(P_{[x,y]})}{s(P_{[x,y]}) + s_{\frac{1}{2}}} \cdot c(P_{[x,y]}), \quad 2.6$$

where the first term is based on ingestion within a cell and $c(P_{[x,y]})$ [-] is the digestibility of the plant material in a cell:

$$c(P_{[x,y]}) = (\exp(-\beta \cdot s(P_{[x,y]})) + \alpha), \quad 2.7$$

where α [-] is base preference for a cell and β [m^{-1}] is the digestibility reduction constant with height (Van de Koppel et al., 1996). Consequently, digestibility is high at low plant density ($1+\alpha$) and declines to α with increasing plant density. Because larger herbivores have a higher tolerance for poor quality forage (Hopcraft et al., 2010) the value of α increases with herbivore size (Fig. 2.1). The relative preference ($f(P_{[x,y]}, P_{\Omega})$ [-]) is the preference of the focal cell divided by the mean preference of the whole grid:

$$f(P_{[x,y]}, P_{\Omega}) = \frac{q(P_{[x,y]})}{\frac{1}{m \cdot n} \cdot \sum_{i=1}^m \sum_{j=1}^n q(P_{[i,j]})}, \quad 2.8$$

Herbivore density in a cell is determined by:

$$h(P_{[x,y]}, P_{\Omega}) = \omega \cdot f(P_{[x,y]}, P_{\Omega}), \quad 2.9$$

where ω [$g \ m^{-2}$] is the regional herbivore density.

In the model herbivores can forage hierarchically, i.e. they select a feeding station (cell) not only based on the preference for that cell but also based on the preference for surrounding feeding stations (De Knecht et al. 2008). We used a convolution method to incorporate this. Convolution is the operation of two functions which produces a new function which is a modified version of one of the first functions. The first function, $q(P_{\Omega})$, is the preference matrix in which each element represents the preference for a cell in the grid. The second function, $k_{[x,y]}$, is a normalized 2D Gaussian distribution. By convoluting matrix $q(P_{\Omega})$ by kernel $k_{[x,y]}$, the new preference of cell $[x,y]$, $u_{[x,y]}(P_{\Omega})$, is influenced by all cells in the matrix, but more so by cells close by:

$$u_{[x,y]}(P) = q(P_{\Omega}) * k_{[x,y]}, \quad 2.10$$

where $*$ is the convolution operator. For a discretized grid equation 2.10 can be rewritten into:

$$u_{[x,y]}(P_{\Omega}) = \sum_{i=1}^m \sum_{j=1}^n q(P_{[i,j]}) \cdot k_{[x-j,y-i]}, \quad 2.11$$

where $k_{[x-j,y-i]}$ is:

$$k_{[x-j,y-i]} = \left(\frac{1}{2 \cdot \pi \cdot \sigma^2} \right) \cdot \exp \left(\frac{-(x-j)^2 + (y-i)^2}{2 \cdot \sigma^2} \right), \quad 2.12$$

where δ [m] is the standard deviation of the Gaussian distribution and thus based on the grain size at which herbivores sample their environment. Because body size positively affects this grain size (Ritchie and Olff 1999), δ is larger for larger herbivores.

When hierarchical foraging was included we determined relative preference by the following equation instead of equation 7:

$$f(P_{[x,y]}, P_{\Omega}) = \frac{u(P_{[x,y]})}{\frac{1}{m \cdot n} \cdot \sum_{i=1}^m \sum_{j=1}^n u(P_{[i,j]})}, \quad 2.13$$

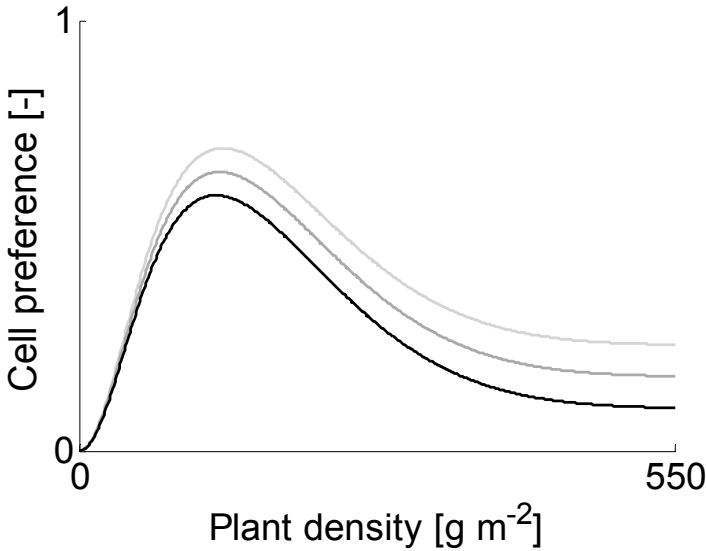


Fig. 2.1 Cell preference as a function of plant density for different-sized herbivores (small, $\alpha = 0.1$ (black), medium, $\alpha = 0.175$ (gray) and large, $\alpha = 0.25$ (light gray))

2.2.2 Simulations and analyses

We simulated with herbivores of different body sizes: small, medium, and large, affecting base preference for a cell (α) and grain size at which the environment is sampled (σ). For all spatial simulations regional herbivore density (ω) was 85 g m⁻², or 1.4 cattle per hectare (600 kg per individual), densities that are found in European nature areas. All simulations were done in MATLAB® (R2010a, The MathWorks 2010), with parameter settings as presented in Table 2.1, and using periodic boundaries. The mosaic was considered stable if the emerging pattern did not change anymore (visual inspection, comparing vegetation height between years). A year in our model corresponds with 200 days, as we assume that the growing season takes 200 days (in line with grazed ecosystems in the temperate zone). Outside the growing season no grazing occurred.

Table 2.1 Parameters used in model simulation

Parameters	Meaning	Value	Units
Plants			
θ	Extrinsic growth rate	0.02 ^a	d ⁻¹
κ	Light extinction coefficient	0.03 ^a	m ² g ⁻¹
l_{half}	Half saturation constant for light	50 ^a	μmol photons m ⁻² s ⁻¹
l_{in}	Incoming light intensity	400 ^a	μmol photons m ⁻² s ⁻¹
δ	Rate of mortality	0.003 ^a	d ⁻¹
p_m	Plant density at s_m	500 ^b	g m ⁻²
s_m	Plant height at P_m	1 ^b	m
d	Clonal invasion rate	1e-4, 1e-3, 1e-2	m ² d ⁻¹
Ungulates			
l	Maximum grazing rate	0.01 ^b	d ⁻¹
s_{half}	Grazing half saturation constant	0.025 ^b	m
α	Base cell preference *	.100, .175, .250	m ⁻¹
β	Digestibility reduction constant	5 ^b	-
ω	Regional ungulate density	85 ^c	g m ⁻²
σ	Sampling grain size	0.5, 1.0, 1.5	m

* for small, medium and large herbivores respectively

a. value based on Huisman and Olf (1998)

b. value based on Bergman et al. (2001)

c. value based on Van Uytvanck et al. (2008)

We gradually increased complexity in our simulations. In our first simulation we did not include hierarchical foraging or clonal invasion to explore if the model could produce stable lawn and rough patches. We investigated how body size affected the capability of herbivores to form a lawn-rough mosaic. Furthermore, we investigated the importance of initial conditions for lawn and rough formation by varying initial plant height. In the next simulation, we added hierarchical foraging and clonal invasion to the model to explore whether this affected the capability of herbivores to form and maintain lawn-rough mosaics. We continued these simulations only with those herbivore sizes that were able to create lawn-rough mosaics. In our last simulations, we added abiotic variation while including all herbivore sizes again. Because we expected that abiotic variation creates a vegetation mosaic in plant height, even when there is no grazing, results were compared to a control simulation without herbivores. Further, as we expected that abiotic variation

creates a vegetation mosaic in plant height, even in the absence of self-facilitation, results were also compared to a second control simulation in which herbivore preference did not decrease with plant height (i.e. α and $\beta = 0$).

2.3 Results

2.3.1 Effect of herbivore size on mosaic formation

We first simulated the model without clonal invasion ($D = 0$), hierarchical foraging or abiotic variation to see if lawn and rough patches emerged in our model with the different-sized herbivore. To explore the importance of initial conditions we started with and without small differences in plant height. Initial differences in plant height were generated using sinusoid function, one initialization representing rough with a high mean plant height ($0.65 \text{ m} \pm 0.02$) (mean \pm coefficient of variance (CV)), and one initialization representing lawn with a low mean plant height ($0.05 \text{ m} \pm 0.04$).

The simulations showed that with small- and medium-sized herbivores a distinct lawn-rough mosaic can be formed as long as small initial differences in plant height exist upon which herbivores can act (Fig. 2.2). It does not matter whether the system starts as one big rough patch (Fig. 2.2B) or one big lawn (Fig. 2.2C). Cells that started with slightly lower plant height attracted slightly more herbivores, which transformed them in lawn. Cells that started with slightly higher plant density attracted slightly less herbivores and therefore decreased in quality, which transformed them into rough patches. Under grazing with small herbivores, the difference in plant height is 6 to 58 cm, and herbivore density is four times higher in lawns. Under grazing with medium herbivores, the height difference is 11 to 41 cm and herbivore density is twice as high in lawns (Fig. 2.2). These mosaics are formed within 25 years and stabilize at 50 years. Hence, in the absence of clonal invasion and hierarchical foraging, abiotic variation is not a necessity for the formation of lawn-rough mosaic as long as there is initial variation in plant height upon which herbivores can act. However, no lawn or rough patches are formed under grazing by large herbivores (Fig. 2.2), because they tolerate low quality (high α) and thus still consume relatively high quantities of rough.

2.3.2. Effect of hierarchical foraging and rough expansion on mosaic maintenance

Because in the simulations of section 2.3.1 only small and medium herbivores can form lawn-rough mosaics we continued with these two body sizes in our second set of simulations. Initial plant height was drawn from a Gaussian distribution ($0.25 \text{ m} \pm 0.02$), so there were no initial patches only some small random variation. We found that hierarchical foraging indeed creates patches, and thus increases spatial heterogeneity, but only in the short run (up to 50 years) (Fig. 2.3). In the long run (> 50 years) hierarchical foraging dissolves small patches and thus leads to a decrease in heterogeneity (Fig. 2.3). With medium herbivores this effect was much stronger and the mosaic was less heterogeneous at its peak (50 years) (Fig. 2.3). Both simulations did not get stable within 1000 years and continued losing heterogeneity.

We continued the next set of simulations with small herbivores, as only these were able to create heterogeneous mosaics with hierarchical foraging in 50 years. We included clonal invasion at three rates (low, medium, high). The peak of heterogeneity is now

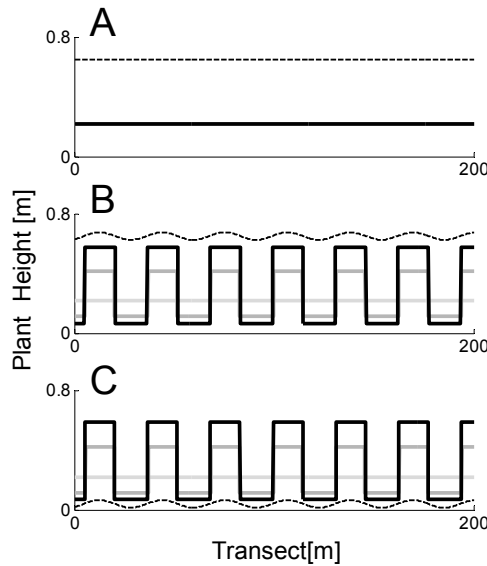


Fig. 2.2 Results at stability ($t = 50$ y) without abiotic variation, clonal invasion or hierarchical foraging with different-sized herbivores (small, $\alpha = 0.1$ (black), medium, $\alpha = 0.175$ (gray) and large, $\alpha = 0.25$ (light gray)). Dashed line is plant height at $t = 0$ y. (A) No differences in initial plant height; (B) differences in initial plant height, with mean = 0.65 m (all vegetation is rough); (C) differences in initial plant height, with mean = 0.05 m (all vegetation is lawn). When initial differences in plant height are present (B, C), small and medium herbivores can form lawn-rough mosaics, no matter if the system starts as one big lawn or rough patch. Without initial differences (A), plant height is equal over the whole transect for all different-sized herbivores.

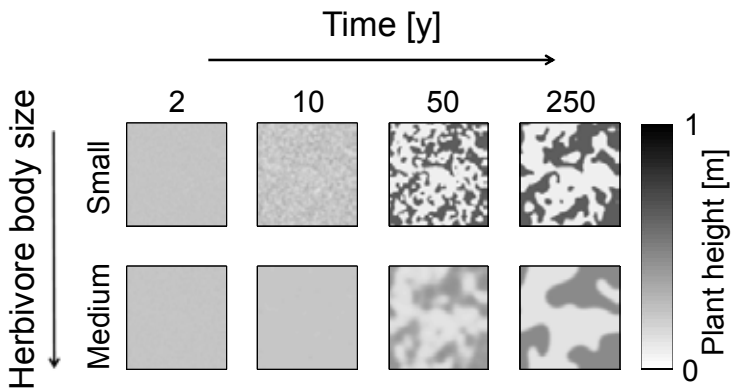


Fig. 2.3 Simulations with hierarchical foraging with small ($\alpha = 0.1$, $\sigma = 0.5$) and large ($\alpha = 0.175$, $\sigma = 1.0$) herbivores, but without clonal invasion or abiotic variation. Starting distribution for plant height was randomly drawn from Gaussian distribution ($0.25 \text{ m} \pm 0.02$) (mean \pm coefficient of variance). Grid size is 150 by 150 cells. Heterogeneity first increases over time (up to 50 years) but the mosaic is not stable and heterogeneity starts to decrease after 50 years. Moreover, the mosaics formed by medium herbivores at 50 years have much lower heterogeneity than the mosaics formed by small herbivores.

already reached in 10 years (vs. 50 years without clonal invasion) (Fig. 2.4). With increasing clonal invasion the mosaics contained less heterogeneity.

Summarizing, in the absence of abiotic variation but with clonal invasion and hierarchical foraging, heterogeneous mosaics can be formed. However, this only happens with small herbivores and low clonal invasion rates. Even under these conditions the emerging mosaic was not stable: it started to lose heterogeneity already after 10 years (Fig. 2.4)

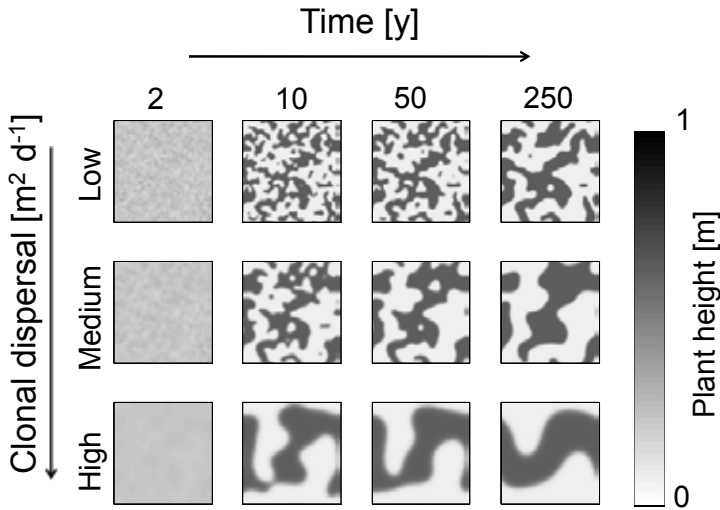


Fig. 2.4 Simulations with only small herbivores ($\alpha = 0.1$, $\sigma = 0.5$), including hierarchical foraging and different rates of clonal invasion ($D=1e-4$ (low), $1e-3$ (medium), $1e-2$ (low)), but without abiotic variation. Starting distribution for plant height was randomly drawn from a Gaussian distribution ($0.25 \text{ m} \pm 0.02$) (mean coefficient of variance). Grid size is 150 by 150 cells. With clonal invasion a lawn-rough mosaics is formed after already 10 years (instead of 50 without clonal dispersal), but the mosaic is not stable and heterogeneity is lost over time. Moreover, with increasing clonal invasion rate the mosaic becomes less heterogeneous at all times.

2.3.3 Mosaic formation and maintenance with abiotic variation

In the next set of simulations we added abiotic variation in combination with hierarchical foraging, and high clonal invasion. To keep the model comprehensible, we simulated abiotic variation by having variation in extrinsic growth rate (θ). Abiotic variation is either spatially random distributed (simulating only small-scale heterogeneity) or spatially autocorrelated (patchy distribution at the spatial scale at which herbivores select their environment). Both spatially random distributed and autocorrelated heterogeneity had the same mean and CV for extrinsic growth rate ($\theta = 0.02 \text{ d}^{-1} \pm 0.13$). We simulated with all three herbivore sizes. Each cell started with the same plant height ($s = 0.25 \text{ m}$).

Adding abiotic variation to our simulations shows that all herbivore sizes, even the large, increase heterogeneity compared to our two controls (absence of herbivores, or without the positive feedback between grazing and quality) (Fig. 2.5). However, only spatially autocorrelated heterogeneity produced heterogeneous mosaics (Fig. 2.5B), not spatially random variation (Fig. 2.5A). Furthermore, adding abiotic variation resulted in stability within 25 years for all simulations.

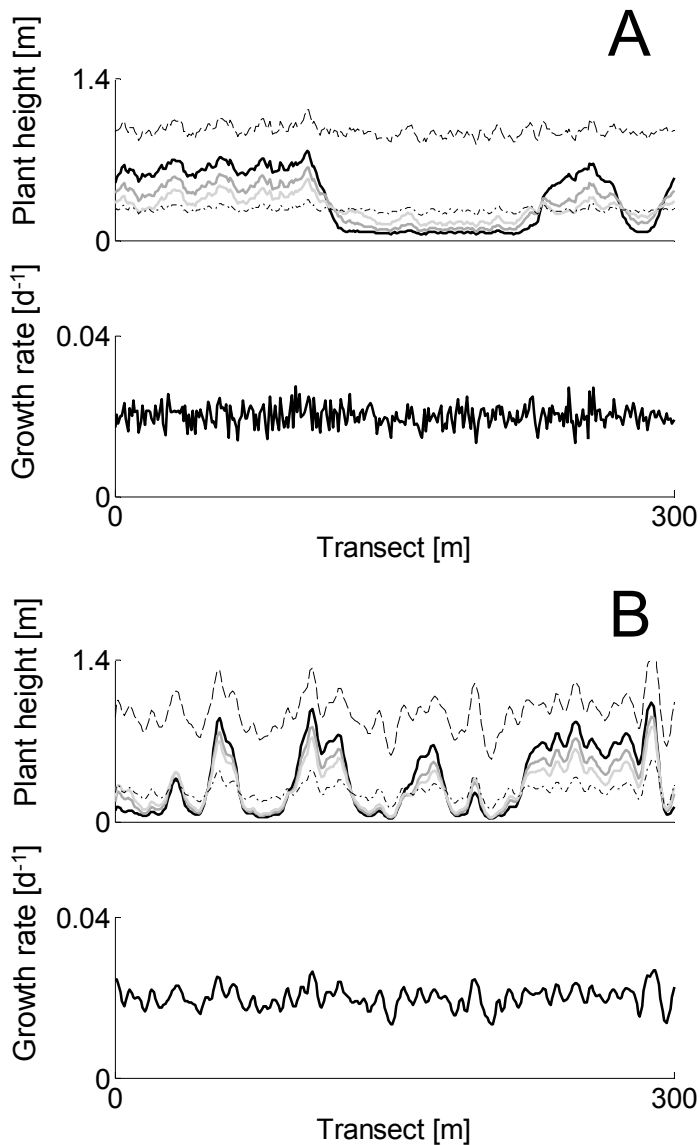


Fig. 2.5 Simulation with hierarchical foraging, high clonal invasion and abiotic variation. Upper panel represents a transect of plant height under grazing of different-sized herbivores (small, $\alpha = 0.1$, $\sigma = 0.5$ (black), medium, $\alpha = 0.175$, $\sigma = 1.0$ (gray) and large, $\alpha = 0.25$, $\sigma = 1.5$ (light gray)). The upper dashed line is when ungulates are absent and the lower dashed line is when grazing does not have a positive effect on quality (both function as controls). The lower panel represents the distribution in growth rate (mimicking abiotic variation). (A) random spatial abiotic variation and (B) spatial autocorrelated abiotic variation (both distributions have the same mean and coefficient of variance). Starting conditions for plant height was completely homogeneous (0.25 m). All simulations are stable within 25 years. In both A and B heterogeneity increases with ungulates compared to the controls, even with large herbivores. However, with random spatial abiotic variation (A) no heterogeneous mosaic emerged because there are only a few large patches. A stable heterogeneous lawn-rough mosaic did emerge with all ungulates with autocorrelated abiotic variation (B).

2.4 Discussion

In this study we explored the potential importance of abiotic variation in interplay with herbivore body size for the formation and maintenance of lawn-rough mosaics. We found that (1) with relative large herbivores the presence of abiotic variation might be essential for the formation of lawn-rough mosaics, but with relative small herbivores, lawn-rough mosaics are generated even in the absence of abiotic variation. However, (2) with both small and large herbivores, abiotic variation may play an important role in maintaining the heterogeneity of lawn-rough mosaics.

Our study suggests that the importance of abiotic variation for vegetation mosaic formation strongly depends on herbivore body size. Especially with large herbivores, abiotic variation seems to be essential for formation. Larger herbivores can survive on lower quality but require higher bulk intake diets while smaller species require higher quality, but sustain on lower bulk intake diets (Bell 1970; Jarman 1974; Demment and Van Soest 1985; Kleyhans et al 2011) Consequently, large herbivores will not react strongly to small differences in plant height, resulting in a homogeneous grazing pattern. Variation in abiotic factors leads to patches of low and high growth rate. Patches with a low growth rate are likely to turn into lawn, while patches with a high growth rate are likely to turn into rough. Our findings suggest that this has to do with the difference in duration of high quality: at low growth rate, it takes a relatively long time before grazed tissue is replaced and before the plant becomes tall with high amounts of structural compounds (low quality tissues such as lignin). Whereas, at high growth rate, it takes a relatively short time before grazed tissue is replaced and before the plant becomes tall with high amounts of structural compounds. Due to the differences in duration of high quality, large herbivores (as well as small herbivores) do react more strongly to small differences in plant height. This sets in motion the positive feedback between grazing and quality, which emerges in lawn formation.

Our results show that with both large and small herbivores, abiotic heterogeneity is important for the maintenance of biotic (vegetation) heterogeneity. In the absence of abiotic variation, small patches have a high risk to disappear, due to hierarchical foraging and clonal invasion. Small lawn patches are intensively invaded by ramets from surrounding rough plants (Kuijper et al. 2004) and are often ignored by herbivores, due to associational unpalatability (Laca et al. 2010; Ritchie and Olff 1999; Atsatt and Dowd, 1976), which decreases their grazing frequency and increases their chance to be converted into rough (McNaughton 1984). Small rough patches are often accidentally grazed together with the target lawn species due to associational palatability (Atsatt and Dowd 1976) which may transform them into lawn. Hence, without abiotic variation, heterogeneity of the mosaics is not maintained (Palmer 1988). However, when small rough patches have a high growth rate, due to abiotic variation, they may remain rough under high grazing because grazed tissue is quickly replaced. When small lawn patches have a low growth rate, they may remain lawn under low grazing frequency (hence not turn into rough) because grazed tissue is only slowly replaced. Consequently, abiotic variation affecting growth rate appears to be important for the maintenance of small-sized patches of both lawn and rough and thus for the maintenance of the heterogeneity of lawn-rough mosaics.

Our model uses two assumptions that may importantly affect the outcome. First it assumes that the abiotic factors are static, whereas in ‘real life’ abiotic factors such as water availability, salinity and soil oxygen are dynamic and interact with biotic factors such as herbivores and plants. For example, trampling by herbivores has been shown to decrease water infiltration and oxygenation of the soil and increase salinity (Hobbs 2006), which would make small lawn patches more stable as it tempers extrinsic growth rate. Furthermore, high plant density increases water infiltration (Rietkerk and Van de Koppel 1997), which would make small rough patches more stable as it increases plant growth rate. It is therefore important to expand our knowledge about the conditions under which herbivores affect abiotic factors. A second model assumption is that plant height has a nonlinear relation with plant density. We implemented this relation as a simple way to model high grazing tolerance of lawns (supplements). A potential biological explanation for this nonlinear relation between plant density and plant height might be the difference in plant architecture between lawn and rough plants. At low plant density lawn plants with a stoloniferous or rosette architecture dominate (Díaz et al. 2007), which translates into high mass-density (plant density/plant height), as most resources are used in for horizontal structures such as stolons and leaves. At high plant density rough plants with a tussock architecture dominate, which translates into a low mass-density, as most resources are used in vertical structures such as stems. This change of mass-density creates the nonlinear relation between plant height and plant density. We propose that investing in horizontal structures is a potential important mechanism of grazing tolerance.

The results of this study have relevant implications for conservation and restoration projects of grazed grasslands in Europe. As shown in our study, herbivores can be used to induce heterogeneous and stable lawn-rough mosaics, with potential positive effects on biodiversity and ecosystem functioning. The success of this approach strongly depends on the presence of abiotic variation in combination with the body size of the herbivore species. Areas that have a high variation in abiotic factors, e.g. riverine areas with small valleys and dunes, may be suitable for management with large herbivores, while in areas with little abiotic variation, e.g. abandoned agricultural areas, smaller herbivores may be more suitable for mosaic formation. However, in the latter case it is questionable how stable these latter mosaics would be over time. Every few decades a reset via temporal exclusion of herbivores may be necessary to maintain heterogeneity in these systems. As temporal exclusions (e.g. for a decade) will reset the system to homogeneous tall vegetation. In the short term, hierarchical foraging will generate patches of different sizes and shapes in this tall homogeneous vegetation, increasing heterogeneity, before associational palatability/unpalatability will dissolve the smaller patches in the long term and thus reducing heterogeneity.

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